Ann. Natal Mus. Vol. 22(3) Pages 913–935 Pietermaritzburg November, 1976

Morphology of the terminalia and known ovipositing behaviour of female Therevidae (Diptera: Asiloidea), with an account of correlated adaptations and comments on phylogenetic relationships

by

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SYNOPSIS

The ovipositing behaviour and morphology of the female terminalia of species within several suprageneric taxa of the family Therevidae are described. The mode of oviposition and oviposition substrate are not easily deduced from a study of the morphology of the female terminalia. A descriptive model relating form (morphology) and function (oviposition) is generated. A phylogenetic assessment of the genus-groups of Therevidae is presented, based on the morphology of the female terminalia and ovipositing behaviour. The *Apsilocephala* group does not easily fit into the concept of the family Therevidae, and, if it is to be retained within the family, it logically has a sister-group relationship to the rest of the Therevidae.

INTRODUCTION

Several factors have prompted this study. The first is that the higher classification of the Therevidae currently being constructed (Irwin & Lyneborg, mss.) is heavily dependent upon morphological features of the male and female terminalia. The second factor is that no one has studied the morphology of the female terminalia in enough detail to adequately describe the main features. The third factor concerns oviposition. Over the years I have observed and noted oviposition patterns of several species of Therevidae (Irwin 1973, in press). Recently, Dr Lyneborg and I, while travelling in the Namib Desert of South West Africa, observed the oviposition behaviour of *Phycus niger* (Kröber). This provided a key which unlocked the sequencing patterns and allowed me to speculate on the phylogeny of the oviposition behaviour. The fourth factor concerns form and function. For many years, various authors (*inter alios* Melin 1923; Hesse 1969; Wilcox & Papavero 1971) have suggested, some more strongly than others, that the mode of oviposition and kind of oviposition substrate of the Asiloidea could be deduced from a study of the morphology of the female terminalia, and vice versa. In theory this always seemed sound, but the facts suggested that the interweaving of form and function—morphology of the female terminalia and ovipositing behaviour—was very complex and one probably could not easily be deduced from the other. The fifth factor concerns the status of the *Apsilocephala*-group, a group whose proper phylogenetic placement in the Therevidae is very much in question. These five factors, woven together, form the fabric of this paper.

The higher classification of the Therevidae is currently undergoing a major revision (Irwin & Lyneborg, mss.) and the hierarchical superstructure therein presented covers all known suprageneric taxa from the Americas, Europe, and Africa. The

Australasian and Oriental Therevidae are very poorly understood and at this time little can be said about their suprageneric classification. For the purpose of this paper, I am restricting the suprageneric hierarchy to two levels, family and genus-group. It is not the purpose of this paper to describe taxa above the genus level. Such descriptions will appear elsewhere.

The genera of Therevidae located within the Ethiopian, Palaearctic, Nearctic, and Neotropical Regions can be clumped into several genus-groups: the *Phycus*-group, *Rueppellia*-group, *Pherocera*-group, *Xestomyza*-group, *Apsilocephala*-group, and *Thereva*-group. For the purposes of this paper, the *Thereva*-group, characterized by enlarged b_1 and b_2 setae on t10 of the female terminalia (figs 1, 2, 14, 33), is treated as a single genus-group even though it comprises four or five distinct subgroups.

This paper deals with the morphology of the female terminalia of the following genera: *Apsilocephala* (*Apsilocephala*-group), *Thereva* and *Irwineilla* (*Thereva*-group), *Lyneborgia* (*Xestomyza*-group), *Phycus* (*Phycus*-group), and *Pherocera* (*Pherocera*-group). The paper also deals with the oviposition behaviour of *Lyneborgia, Pherocera, Thereva,* and *Phycus*. The morphology of the female terminalia neglected the *Rueppellia*-group; the oviposition behaviour sequences lacked observations on members of the *Rueppellia*-group and the *Apsilocephala*-group. Otherwise, all genus-groups, save some within the *Thereva*-group complex, are treated.

Observations of oviposition sequences reported were made in the laboratory using glass-sided terraria with relatively fine-grained, sandy substrates. Most observations were made during the late morning hours. *Phycus niger*, however, oviposited late in the evening. This was attributed to the fact that the ovipositing female was captured indoors and was probably under physical pressure to oviposit.

Following is a list of abbreviations used in the text and figures:

a	anus	**ov**	median or common oviduct
ag	accessory gland	**sm**	sclerotized membrane
b_1	posterior dorsolateral bristles of t10	**sp**	spermatheca
b_2	anterior ventrolateral bristles of t10	**su**	subanal plate
c	cercus	**s8**	sternite eight
fur	furca (vaginal apodeme, s9)	**t8**	tergite eight
ga	genital aperture	**t9**	tergite nine
gc	genital chamber	**t10**	tergite ten
pg	penial guide	**t9+10**	compound tergites nine and ten

MORPHOLOGY OF THE FEMALE TERMINALIA

The female terminalia, as herein discussed, comprise the genital and postgenital segments (abdominal segments eight to eleven).

Segment eight

Tergite eight.—On the expanded female abdomen, tergite eight (t8) is a medium-sized, easily observable sclerite which commonly overlaps sternite eight (s8) (figs 12, 14, 16, and 18). Although varying in shape between genus-groups in accordance with the shape of s8, t8 is a relatively stable, unmodified sclerite. Because the anterior portion of tergite nine (t9) is completely membranous in some genera, the connection between t8 and t9 can be difficult to detect.

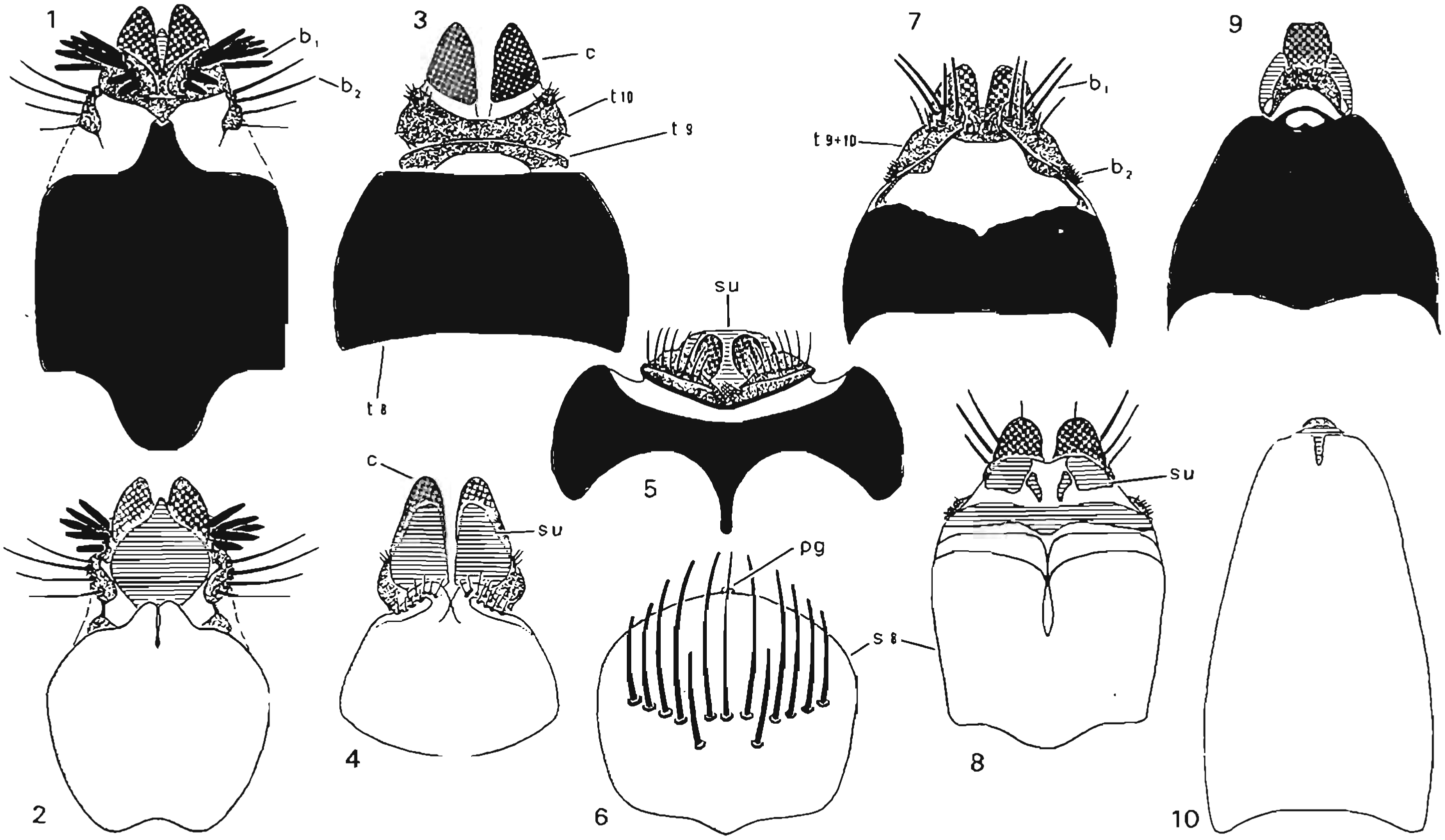
The shape of t8 varies greatly between genus-groups of Therevidae, a gross overall measure of which is the ratio of medial length to maximum width. Since the normal ratio of length/width of preterminal tergites (e.g. six and seven) is usually between 0,6 and 0,8—that is slightly wider than long—I am assuming that this represents the plesiomorphic state. *Apsilocephala* (fig. 3) with a ratio of 0,6 and t8 of relatively unmodified shape appears plesiomorphic. While *Pherocera* (fig. 9) with a ratio of 0,8 also falls within the plesiomorphic range, its sharply tapered apex is definitely an apomorphic adaptation. Those genus-groups with a ratio of less than 0,6 (*Phycus* fig. 7 with a ratio of 0,5; *Lyneborgia* fig. 5 with a ratio of 0,4) are apomorphic. At the same time, *Thereva* (fig. 1) with a ratio of 1,0 or greater is apomorphic. Therefore, it seems to me that two evolutionary trends occur with respect to the shape of t8, those with elongated, narrow shapes and those with broad, squat shapes. *Apsilocephala* does not fall within either trend and is considered plesiomorphic in this respect.

Sternite eight.—Like t8, s8 is a relatively large and conspicuous sclerite. Because it functions variously as a housing for the furca, as a digging–anchoring apparatus for oviposition, and as a guide for penial insertion during copulation, it is a more complex structure than t8 and has undergone diverse modifications.

The posterior portion of s8 is almost always modified in some way. A *medial slit* is usually present through which the penis enters the genital chamber during copulation (figs 2, 8, 13). In some species this slit becomes fused posteriorly, resulting in a secondary aperture. Variation in slit-size and complexity can be seen in closely related species, indicating that slit modification might be a good species or species-group character but not a good generic or suprageneric character.

Along the inner-medial surface of s8 and attached or proximal to the medial slit is a small sclerite, undoubtedly derived from s8, which I have termed the *penial guide* (pg) (figs 11, 13, 17, 19). The penial guide is incompletely attached to s8 at the internal medial slit orifice and extends anteriorly to a point slightly anterior to the common spermathecal aperture in the roof of the genital chamber. The sclerite, sometimes consisting of two flaps, is variously shaped, and, from the several dissections I have made, curves dorsad into the genital chamber and peaks just short of the spermathecal aperture. Although as yet unproven, the penial guide possibly functions as a brace and guide which, during copulation, inclines the penis dorsad at an angle which, upon ejaculation, directs the sperm into the spermathecal aperture and ducts.

Of the various groups of Therevidae examined by me, only *Apsilocephala* lacks a penial guide (fig. 15). The female of *Apsilocephala* possesses an extremely long, accordion-shaped, large-orificed spermathecal duct (fig. 21). A possibly correlated feature of the male is an extremely elongate aedeagus which is coiled within the abdomen except during copulation. Although unobserved, it seems probable that during copulation the aedeagus enters the aperture of the spermathecal duct and extends into the common spermathecal duct. If this occurs, sperm enters the sperma-



1–10. Female terminalia of Therevidae. 1–2, *Thereva* sp.; 3–4, *Apsilocephala* sp.; 5–6, *Lyneborgia ammodyta* Irwin; 7–8, *Phycus niger* (Kröber); 9–10, *Pherocera flavipes* Cole. Odd-numbered figures, dorsal view; even-numbered figures, ventral view.

theca directly. Even though the presumed function of the penal guide (i.e. to direct the angle of ejaculated sperm) is bypassed in *Apsilocephala*, it would be speculation on my part to assume that the penial guide had been lost, or, for that matter, that it had never existed. Whatever the case, this difference between *Apsilocephala* and other Therevidae is noteworthy.

Apart from the medial slit and the penial guide, major modifications of the posterior portion of s8 are confined to discrete taxonomic sectors of the Therevidae. The *Xestomyza*-group including *Lyneborgia* is characterized by a sharply angulate apical upcurve of s8 and a horizontal row (or rows) of very strong, elongate setae immediately anterior to the angulate upcurve (fig. 12) (Lyneborg 1972; Irwin 1973). These modifications evolved with the peculiar oviposition behaviour of the group (see below).

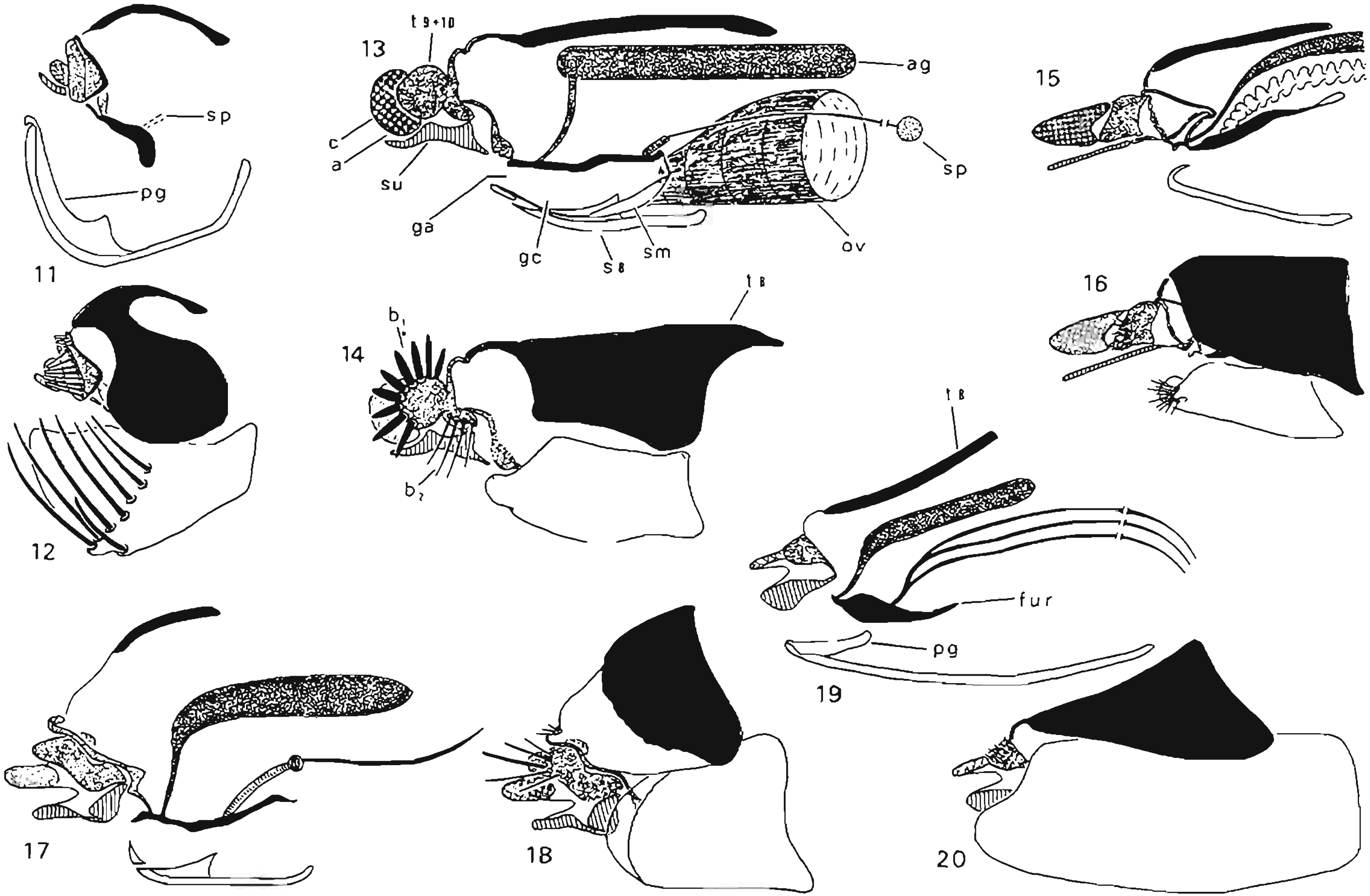
Some genera of the *Thereva*-group, on the other hand, have at the posterior portion of s8 a medial hump-like knob (or pair of knobs) which surrounds or forms the lateral margins of the medial slit. Generally clothed in short, stiff hairs, the hump-like structure probably acts as a digging apparatus during the oviposition sequence. While the female of *Apsilocephala* (figs 4, 16) possesses a structure of similar design and probably of similar function as that of the female of many *Thereva*-group genera (figs 2, 14), I consider that the modification arose independently. The knob-like outgrowths of the *Thereva*-group, in other words, are probably not homologous to the semi-detached, flap-like processes of *Apsilocephala.*

Within the genital chamber and between the posterior margin of s8 and the anterior margin of the furca (fur) or vaginal apodeme, and to my knowledge confined to the *Thereva*-group, are two laterally placed semisclerotized membranes. In some genera they form definite sclerites (sm) which cradle the posterior portion of the common oviduct (ov) (fig. 13). Since the furca is undoubtedly a remnant of sternite nine (Bonhag 1951), the membrane almost certainly represents the intersegmental membrane connecting sternites eight and nine.

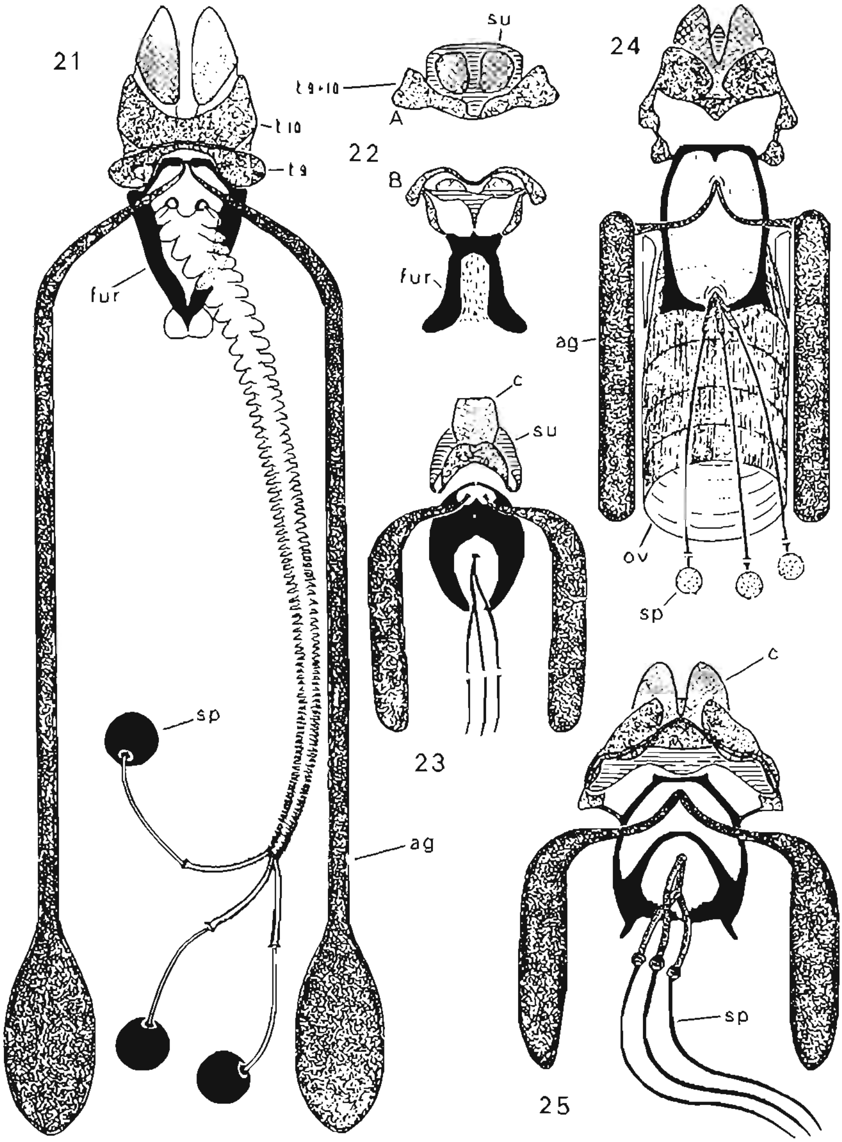
Segment nine

Tergite nine (*and tergite ten*).—Within the Therevidae the modification of tergite nine (t9) and tergite ten (t10) cannot be entirely separated for they often are fused sclerites. In figs 1, 5, 7, 11–14, 17, 18, 22, 24, and 25, t9 and t10 have been depicted as a common sclerite (t9+10) even though two distinct, though often fused, segments are involved. Only when specimens with a more plesiomorphic t9 and t10 are examined, can an appreciation of the evolution of these two tergal elements be gained. To this end, I have examined a number of brachycerous flies, especially those within the superfamilies Tabanoidea and Asiloidea.

An examination of a very primitive member of the family Tabanidae, *Phara bivirgulata* Austin, provided a probable plesiomorphic model for the whole of the lower Brachycera (*see* Stuckenberg 1973, for phylogenetic discussion of the lower Brachycera). In this species of *Phara*, t9 and t10 are distinct, separate and undivided sclerites (figs 26, 27); the posterolateral margins of t9 are extended ventrally and fused with the posterolateral margins of the furca (fur) (fig. 27). *Suragina bezzii* (Curran) (figs 28, 29), a member of the tabanoid family Athericidae, possesses the same basic structures



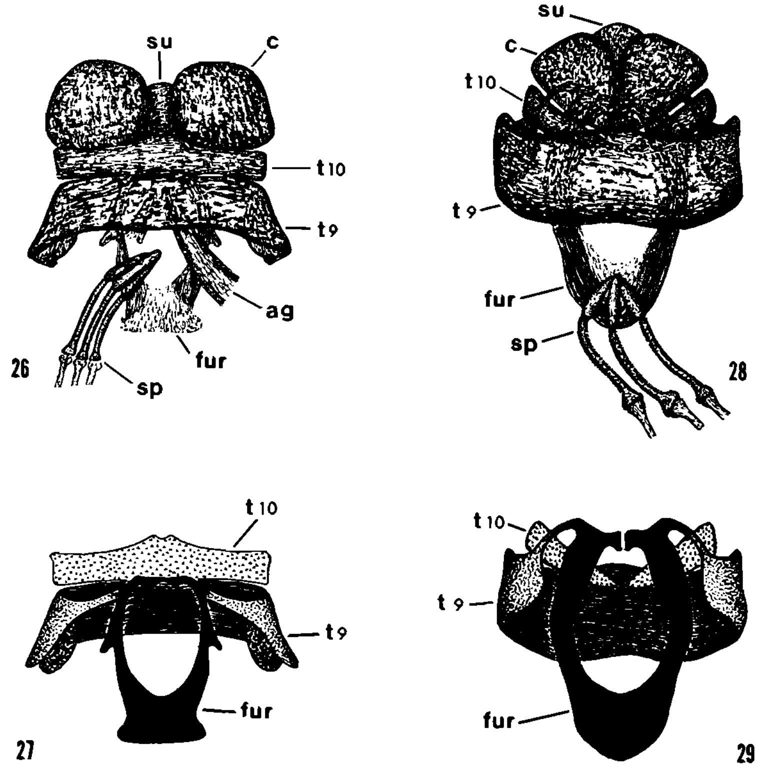
11–20. Female terminalia of Therevidae, lateral view. 11–12, *Lyneborgia ammodyta* Irwin; 13–14, *Thereva* sp.; 15–16, *Apsilocephala* sp.; 17–18, *Phycus niger* (Kröber); 19–20, *Pherocera flavipes* Cole. Odd-numbered figures, cut-away view; even-numbered figures with segment 8 entire.



21–25. Female terminalia of Therevidae, dorsal view. 21, *Apsilocephala* sp.; 22, *Lyneborgia ammodyta* Irwin (A, dorsal view; B, view showing furca in horizontal position, rotated nearly 70°); 23, *Pherocera flavipes* Cole; 24, *Thereva* sp.; 25, *Phycus niger* (Kröber).

as *Phara* except that, in *Suragina*, t10 has become medially split into two lateral sclerites. This development represents an apomorphic modification within the Tabanoidea.

The divided t10, however, appears to be plesiomorphic within the Asiloidea. After having examined female terminalia from the following asiloid families, I was

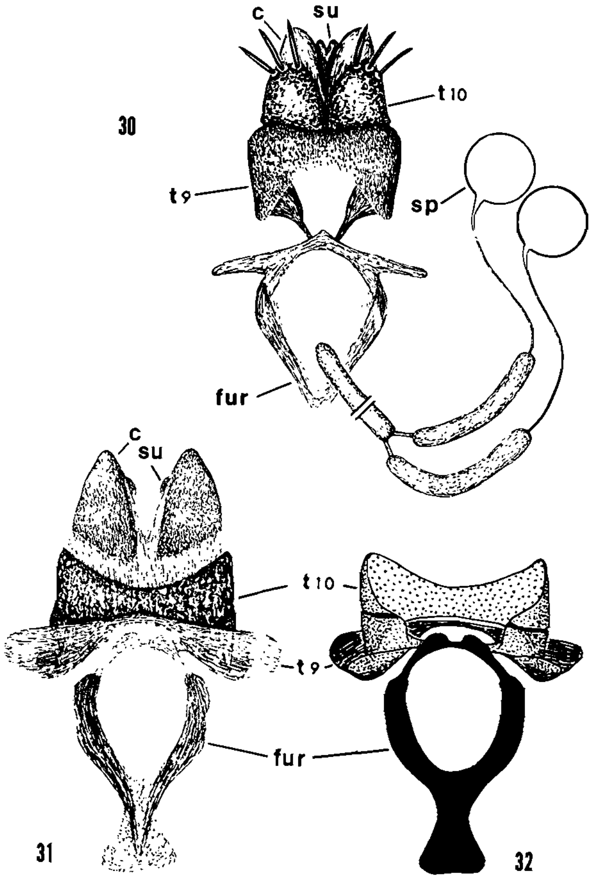


26–29. Female terminalia of lower Brachycera. 26–27, *Phara bivirgulata* Austen (Tabanidae); 28–29, *Suragina bezzii* (Curran) (Athericidae); 26 & 28, dorsal view; 27 & 29, ventral view of tergites 9 and 10 and furca.

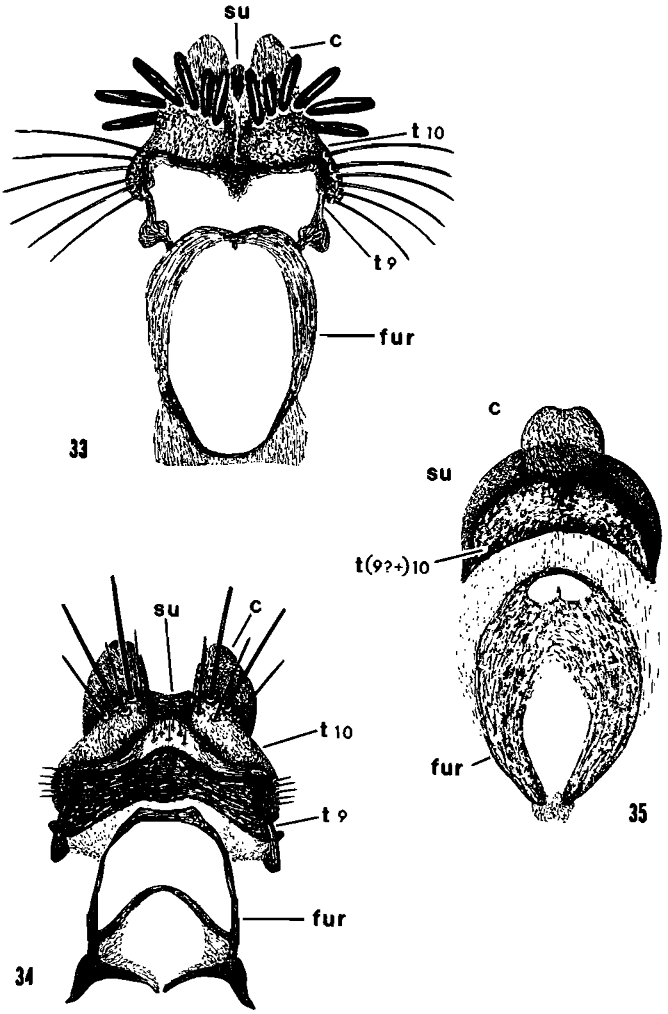
unable to find a single instance (other than *Apsilocephala* mentioned below) where t10 was either undivided or was not entirely fused with t9 (for example see *Pherocera flavipes* below): heterotropine Bombyliidae, Apioceridae, Mydidae, Asilidae, Scenopinidae. T9 and t10 are undoubtedly separated plesiomorphically in Asiloidea. Furthermore, t9, in its plesiomorphic state, is undoubtedly posterolaterally fused to the furca. Andersson (1974: 34 and fig. 18) in his discussion of the female of *Glabellula arctica* (Zett.) (Bombyliidae: Cyrtosiinae) states that, 'Under [*sic* dorsad of] sternite 8 there is a furca, the apical corners of which are connected with tergite 9'. The heterotropine *Prorates frommeri* Hall currently placed within the family Bombyliidae (Hall 1972) illustrates the probable plesiomorphic state for t9 and t10 within the female terminalia of the Asiloidea (fig. 30).

The Therevidae, a family within the Asiloidea, shows strong homologies in the female terminalia with *Prorates* and other members of the Asiloidea. In *Thereva plebeja* Linn., for instance, t10 is divided, t9 is undivided and its lateral margins are fused with the posterolateral margins of the furca (fig. 33). T9, however, has become a narrow, rod-like sclerite partially fused with t10 (fig. 33). There are similar developments in *Phycus niger* (Kröber) (fig. 34) and in *Lyneborgia ammodyta* Irwin (not illustrated). Both possess a divided t10, and a narrow, rod-like t9 that is at least partially fused with t10. In *Lyneborgia*, furthermore, t9 is fused laterally with the posterolateral margins of the furca (fig. 22B). In *Phycus*, however, the ventral extensions of the lateral margins of t9 do not fuse solidly with the furca (fig. 34). Instead, a semi-sclerotized, membranous union is formed. *Pherocera flavipes* Cole (fig. 35) carries this line of evolution even further: the sclerites forming t9 and t10 have, in all probability, solidly fused, and, at the same time, the ventral extensions of t9 have atrophied and the union between t9 and the furca has become membranous (fig. 35). The lateral margins of t9+10 have, in fact, become hinged to the anterolateral margins of the subanal plate.

Apsilocephala (figs 31, 32) remains an anomaly in many respects. Though t9 is completely membranous, t9 and t10 are not fused and in this respect are similar to *Prorates*. Likewise, t9 has posterolateral extensions which fuse with the posterolateral margins of the furca. The mechanism by which t9 and the furca unite, however, appears unique to the Asiloidea (fig. 15). Furthermore, t10 is an undivided sclerite; this, as mentioned above, coupled with distinct t9 and t10, is not known to me in



30–32. Female terminalia of Brachycera. 30, *Prorates frommeri* Hall, dorsal view; 31–32, *Apsilocephala* sp. 31, dorsal view; 32, ventral view of tergites 9 and 10 and furca.



33–35. Female terminalia of Therevidae, dorsal view. 33, *Thereva plebeja* Linnaeus; 34, *Phycus niger* (Kröber); 35, *Pherocera flavipes* Cole.

the Asiloidea. Therefore, in at least two respects mentioned above, *Apsilocephala* stands apart not only from the Therevidae but, to my knowledge, from the Asiloidea.

Sternite nine.—Bonhag in his discussion of the adult female horsefly, *Tabanus sulcifrons* Macq. (Tabanidae) (1951: 56), states that, 'Invagination of the region immediately behind the eighth abdominal sternum has carried the sternum of the ninth abdominal segment inward. The pouch formed by this invagination is the genital chamber which leads to the external opening of median oviduct. . . . The roof of the genital chamber is formed by the invaginated venter of the ninth abdominal segment and the lateral sclerites of the roof of the genital chambers are sternites of the ninth abdominal segment. . . . Much support can be given to the opinion that the roof of the genital chamber represents the venter of the ninth abdominal segment. The dorsoventral muscles of the ninth abdominal segment are inserted on the lateral sclerites of the roof of the genital chamber and, since these muscles are always inserted on the sternal plates of their respective abdominal segments, the lateral sclerites are undoubtedly sclerites of the ninth segment. The posterior attachment of the muscle that seems to be the vaginal longitudinal muscle of segment eight (retractor-depressor of the genital chamber) also strengthens this interpretation. Finally, sagittal sections of the tip of the abdomen show that the roof of the genital chamber intervenes between the eighth abdominal sternum and the venter of the proctiger (sterna X and XI); thus the roof of the genital chamber occupies the position in the sequence of sternal plates, normally occupied by the ninth abdominal sternum.' The fusion between the ventral extensions of the posterolateral (lateral in Therevidae) margins of t9 and the posterolateral margins of the sclerites forming the roof of the genital chamber, or furca, lend even more support to the thought that the furca represents the sclerites of the ninth abdominal sternum. The sclerites forming the roof of the genital chamber, the furca and the vaginal apodeme are, in fact, all homologues of the sclerotized portion of sternite nine. For convenience, I am herein referring to the sclerites forming sternite nine as the furca (fur).

The furca consists of two lateral sclerites whose anterior ends are always, and whose posterior ends are often, connected by a sclerotized bridge or bar. Stretched between the three- or four-sided sclerotized framework is a membranous sheath through which pass the ducts of the spermathecae and the accessory glands. These ducts open into the genital chamber (fig. 13). In Therevidae, to my knowledge, there is always a single pair of accessory glands (ag) which generally empty as two separate apertures through the posteromedial membranous sheath of the furca (figs 21, 23–25). The spermathecal ducts usually form a single aperture in the anteromedial portion of the membranous sheath (figs 13, 19, 21, 23–25, 28, 30).

Phara (fig. 26) and *Suragina* (fig. 28), herein representing primitive tabanoids, have three spermathecae. Mühlenberg (1971*a*: 10) reports that all bombyliids possess three spermathecae, but *Prorates* appears to have two (fig. 30). Owsley (1946), in reviewing the literature concerning spermethecae in Asilidae, found that the overwhelming majority of asilids possessed three spermathecae, and that only within the genus *Proctacanthus* were two spermathecae detected. Irwin & Stuckenberg (1972) reported two unsclerotized spermathecae in the apiocerid, *Tongamya miranda* Stuckenberg. It seems almost certain that within the Tabanoidea and Asiloidea, three spermathecae represents the plesiomorphic state.

From the material at hand it seems probable that all female therevids possess three spermathecae. These elements are very thinly sclerotized and are not easily traceable in dissected specimens, except that in *Apsilocephala* the three spherical spermathecal receptacles are heavily sclerotized (fig. 21) and easily visible in the macerated female abdomen. In *Pherocera* and *Phycus* the three spermathecae arise from the dorsal surface of the membranous furcal sheath in various branching sequences and extend anteriorly into the abdomen as three ducts which taper to fine points apically (figs 19, 23, 25). I was unable to locate any unbroken spermathecal ducts in *Lyneborgia* (fig. 22B), but I would expect them to be of a similar construction to those of *Phycus* (fig. 25). Each of the three thinly sclerotized spermathecal ducts in the *Thereva*-group terminates in a rounded, very thinly sclerotized apical sperm receptacle. In *Irwiniella natalensis* (Kröber), the sperm receptacles are covered internally with short, sparse setae (figs 13, 24).

In view of the shapes of the furcae in Tabanidae (figs 21, 22), Athericidae (figs 23, 24), and the heterotropine genus *Prorates* (fig. 30), the probable plesiomorphous shape of the furca is elongate-ovoid. This, with certain modifications, occurs throughout the *Thereva*-group (figs 24, 33). This shape is also found in *Apsilocephala*, with a membranously modified posterior bridge (fig. 31). Structural modifications have occurred in the *Phycus*-group, the *Xestomyza*-group, and the *Pherocera*-group. In the *Phycus*-group a horizontal, sclerotized bar has formed through the membranous sheath at a point posterior to the spermathecal aperture and anterior to the accessory gland apertures (figs 25, 34). The horizontal bar has become extensively thickened and dominant in the *Pherocera*-group (figs 23, 25). Both the horizontal bar and the anterior bridge of the furca seem to have atrophied in the *Xestomyza*-group as represented by *Lyneborgia* (fig. 22B).

Segment ten

Tergite ten.—The evolution of tergite ten (t10) has been discussed under t9, above. One further aspect, setal modifications and patterns, requires consideration. From the previously mentioned examples of Tabanoidea, *Phara* (fig. 26) and *Suragina* (fig. 28), it seems possible that, at least within the Tabanoidea, a single naked sclerite forming t10 represents the plesiomorphic state. The Asiloidea present a more complex picture. With the exception of certain Therevidae (e.g. *Pherocera*), all examined species of asiloid females which are known or presumed to oviposit in sandy or loamy substrates possess modified setae on t10 (i.a. Melin 1923). In these cases, t10 is often referred to as an *acanthophorite*. Conversely, those which oviposit in other situations, such as in the air, in logs, and in plant parts, seem to lack modified setae, except, of course, the Bombyliidae proper which take fine sand particles into the genital chamber and therewith coat the eggs (i.a. Bibliotti, Demolin & Du Merle 1965; Mühlenberg 1968, 1971*b*; Hull 1973; Havelka 1974). The occurrence on a similar portion of t10 of specialized or unspecialized setae in some members of almost all asiloid families leads me to believe that unspecialized setae on t10 might well be plesiomorphic, and that the lack of and specialization of setae (e.g. further enlargement and modification of setae on t10) probably represent apomorphic states.

Within the Therevidae, all groups have t10 setae modified in some respect. For instance, all females of the *Thereva*-group have distinctly thickened spines in the posterodorsal position (fig. 1, b_1) and more elongate setae in the anteroventral position (fig. 1, b_2). The *Xestomyza*-group possess relatively unspecialized setae in a row along the entire face of each sclerite forming t10 (fig. 5) in the few species I studied. Another smaller set of setae is located centrally on the semisclerotized membrane fusing t9 and t10. This central set of setae is probably homologous with that occupying a similar position in *Phycus niger* (Kröber) (fig. 7) and, in fact, belonging to t9. Females of the *Phycus*-group have rather unspecialized setae, but they occupy discrete sections of t10: larger, thicker setae posteromesally (fig. 7, b_1), and smaller, thinner setae anterolaterally (fig. 7, b_2). Females of the *Pherocera*-group possess small, very unspecialized setae scattered over t9+10 (fig. 9). *Apsilocephala* has t10 practically bare of setae; a few short, thin setae occur mainly on the posterolateral margins (fig. 3).

Within the range of forms presented by the species used in this study, it seems probable that the setae typified by *Phycus niger* (figs 7, 34) represent only a slight apomorphic modification from the plesiomorphic state. It seems probable that medium-sized setae over the entire dorsal surface of t10 is plesiomorphic. The *Thereva*-group then, represents extreme apomorphy towards a digging-anchoring function of the t10 setae, and *Pherocera* represent extreme apomorphy towards a streamlined t10 lacking setae. *Lyneborgia*, representing the *Xestomyza* group, typifies another slight divergence from the plesiomorphic state. *Apsilocephala*, with respect to t10 setae, seems relatively plesiomorphic and does not easily fit into the picture of Therevidae.

Sternite ten (+eleven).—Sternite ten (+eleven), the ventral portion of the proctiger, is herein termed, in keeping with standard terminology, the *subanal plate* (su). It is undoubtedly a single, medium-sized sclerite in its plesiomorphic state. This can be supported by noting that the subanal plate in the tabanid *Phara* (fig. 26), and the athericid *Suragina* (fig. 28), is a single, posteriorly rounded sclerite. Furthermore, the heterotropine *Prorates* (fig. 30), and the therevids, *Thereva* (fig. 2), *Lyneborgia* (fig. 5), and *Pherocera* (figs 9, 35), possess similar, though variously modified, subanal plates. *Phycus* (fig. 8) has a similar subanal plate, but the sclerite has broken up into several island sclerites in a semimembranous field. It is, in fact, only in *Apsilocephala* that the subanal plate is longitudinally divided (fig. 4), and even in this genus, a membrane connects the two sclerites (fig. 31).

Cerci.—The cerci are attached to the posterior margin of t10 and may represent appendages of t10 even though embryological evidence points to the possibility that the cerci are appendages of the atrophied tergite eleven (Bonhag 1951: 158). In their plesiomorphic state, the cerci consist of a pair of flap-like, disc-shaped sclerites located above the anus. All tabanoids herein discussed have this arrangement (figs 26, 28), as does *Prorates* (fig. 30). In fact, all *Thereva*-group (figs 1, 33), *Xestomyza*-group (fig. 5), and *Phycus*-group (figs 7, 34) females have this arrangement. In the *Pherocera*-group (figs 9, 35) the cerci have fused into a single sclerite, obviously an apomorphic state.

OVIPOSITION BEHAVIOUR

Within the Asiloidea, oviposition behaviour has been reported for several genera of Asilidae (i.a. Melin 1923), and a few genera of Bombyliidae (i.a. Bibliotti, Demolin & Du Merle 1965; Mühlenberg 1971*a*; Hull 1973), Mydidae (i.a. Hesse 1969; Wilcox & Papavero 1971), Apioceridae (Cazier 1963; Irwin & Stuckenberg 1972), and Therevidae (Irwin 1973, in press *a*). No account of oviposition in the Scenopinidae has come to my attention and the above-cited reports of oviposition in Mydidae and Apioceridae were incomplete and lacked detailed analysis. Hemmingsen & Nielsen (1971) described the sequencing steps involved in the oviposition pattern of various species within the Vermileoninae (Tabanoidea: Rhagionidae). Although not included within the Asiloidea, the pit-digging behaviour displayed by ovipositing females is in certain respects convergent with that of certain oviposition behaviour in *Phycus* and *Pherocera*. I shall elaborate on this below.

I have described the oviposition sequences of *Lyneborgia ammodyta* Irwin (*Xestomyza*-group) (Irwin 1973), and three species of *Pherocera* and one species in a closely related new genus (*Pherocera*-group) (Irwin, in press *b*). Observations on the oviposition behaviour of various species within the *Thereva*-group were noted over a ten-year period. In February 1974, Dr L. Lyneborg and I compiled notes on the oviposition behaviour of a South West African species, *Phycus niger* (*Phycus*-group). Most of the genus-groups are represented in the above records (the *Rueppellia*-group and *Apsilocephala*-group are missing) and this has made it possible to speculate on the evolutionary trends of the oviposition behaviour in the family Therevidae.

From my various observations, the range of variation in oviposition behaviour between different species and genera of any given genus-group is slight. Furthermore, variation between closely related groups is moderate while that between distantly related groups is great. This conclusion is based upon four observations of four species in three genera of the *Thereva*-group, approximately twenty observations of four species in two genera of the *Pherocera*-group, two observations of one species in the *Xestomyza*-group and one observation of one species in the *Phycus*-group. including over ten ovipositional sequences. (A single observation indicates from one to many ovipositional sequences viewed continuously.) These observations convinced me that each oviposition sequence reported below of four species in four different genus-groups is for the most part representative of the genus-group as a whole.

I have, for the purpose of convenience, divided the oviposition sequence into five discrete phases: approach, stance, insertion, egg-laying and withdrawal. *Approach* refers to the activity-pattern the fly performs prior to selecting the exact oviposition site. The approach pattern is a walk and can in some instances be accompanied by various sensing movements. *Stance* refers to the attitude assumed by the female upon termination of the approach phase and just prior to the activity-phase which is directed towards placing the abdomen in the proper position for egg-laying. *Insertion* comprises a combination of actions all directed towards placing the tip of the abdomen in the proper attitude and location for actual egg-laying. *Egg-laying* refers to the actual muscular contractions of the abdomen which culminate in the ejection of a single egg from the genital chamber. This phase is the same in all species studied and will not be dealt with further in this paper. *Withdrawal* refers to the removal of the abdomen from the egg-laying position and any subsequent action involved with the last-laid egg. This phase sometimes includes the filling-in of an oviposition pit. There are other factors of the oviposition sequence which will not be dealt with in this paper: namely, rests and timing. They are important elements of the sequence, but both vary enormously, depending not only on the taxon involved, but equally on how tired a specimen becomes through time.

Oviposition sequences of four species of Therevidae

Thereva spp. (*Thereva*-group) [southern California]

Approach. Direct, without any noticeable searching or sensing movements. The female alighted on the substrate, walked forward a few centimetres and began the next phase in the sequence.

Stance. Upright, abdomen curved downward contacting substrate with hind legs spread outwards and slightly hindwards.

Insertion. The female embedded her abdomen by boring and contorting it until three-quarters to the whole length was in the substrate.

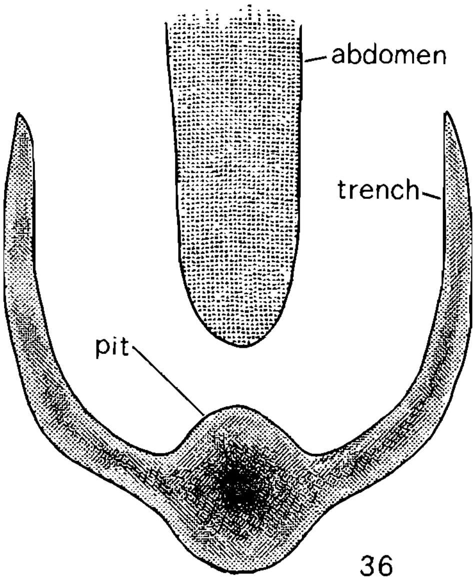
Withdrawal. As soon as the egg was laid, the abdomen was withdrawn.

Phycus niger (Kröber) (*Phycus*-group) [South West Africa]

Approach. Direct without any searching movements. The female landed on the substrate, walked backwards a few millimetres, and began the next stage.

Stance. Head high, antennae stretched forward and slightly elevated; body high off substrate; abdomen arched with its tip directed downward and contacting substrate. Hind legs extended hindward so that tarsi were almost touching one another about four millimetres behind the tip of the abdomen.

Insertion. The hind legs were alternately pulled forward under the abdomen and returned to the outstretched position. Each time a leg was brought forward it scooped some sand from an area just behind the tip of the abdomen and deposited it under the abdomen. About five short, rapidly executed spurts of digging activity completed the one-centimetre deep pit. These five spurts of activity lasted approximately 14 to 18 seconds. As soon as the pit was completed, the leg motion changed, becoming slower, and the digging action shallower. The hind legs moved anteriorly and laterally outwards until an arc was completed, the tarsi level with the tip of the abdomen but extended two to three millimetres to either side. At this point the legs, still slowly and shallowly digging, moved anteriorly and parallel to the sides of the abdomen for about one third of its length. In effect, an arc-like trench (fig. 36) had then been dug on each side of the central, deeper pit. The trench digging lasted five to ten



36. *Phycus niger* (Kröber). Dorsal view showing diagrammatically the abdomen, oviposition pit and trench.

seconds; a one to two seconds rest followed trench digging, after which, the female began a slow, backwards-directed walk with a staccato motion. An egg was laid as the abdomen made contact with the far pit-wall.

Withdrawal. The staccato movements continued as the fly moved backwards for another five to six millimetres. This action by the abdomen against the pit-wall caused the pit to collapse and the egg to be buried. The stage lasted about two or three seconds.

Pherocera flavipes Cole (*Pherocera*-group) [southern California]

Approach. Indirect, with searching movements. The female landed on the substrate and walked forward on her hind two pairs of legs in a slightly meandering line, her forelegs outstretched and waving from side to side just above the substrate. The tip of her abdomen was lightly dragged over the sand. At the end point of the approach, the female halted, turned about so that the tip of her abdomen was placed directly over the area last explored by the forelegs.

Stance. Head high, abdomen low with its tip resting on the substrate. Fore legs to the sides and slightly in front of the head; middle legs to the sides and slightly behind thorax; hind legs to the sides and behind tip of abdomen.

Insertion. The hind legs were alternately and rapidly pulled forward under the thorax and returned to the outstretched position. Each time one was brought forward, it scooped some sand from below the tip of the abdomen and deposited it under the thorax. As the process continued, a pit was dug and the sand built up under the thorax. The tip of the abdomen remained in contact with the pit-bottom. The female stopped digging when the pit was approximately three millimetres deep. She then thrust her abdomen into the bottom of the pit so that it was nearly completely buried in the sand. She then rested for a few seconds.

Withdrawal. As the abdomen was withdrawn, the hind legs alternately pushed the pile of sand from under the thorax into the pit. This action continued until the pit was entirely filled in.

Lyneborgia ammodyta Irwin (*Xestomyza*-group) [South Africa]

(*Note:* Females of this genus are exceptional in the family because they have reduced wings and are flightless.)

Approach. Direct, without noticeable searching movements. The female walked forward, using only the fore and middle legs; the hind legs were limply dragged behind. The abdomen was arched outward and bent strongly downward at the tip so that the apex contacted the substrate.

Stance. Head high, body high off substrate, abdomen high and arched sharply downward at tip, contacting substrate. Fore legs were held to the sides and slightly in front of the head; middle legs to the sides and slightly behind the thorax; hind legs to the sides and outstretched behind the abdomen.

Insertion. The hind legs alternately tensed, but instead of pulling forward and scooping sand, they held their positions and the consequent tensing seemed to help force the tip of the abdomen into the substrate. Along with this action, the fly contorted her abdomen and this aided in embedding the tip into the substrate. These actions continued until the abdomen was nearly half-buried, this producing a body-line angle of 45° to the horizon. At this point the female reared up so that the only contact with the substrate was her embedded abdomen; the body-line formed an angle of 85 to 90° with the horizon and her short, highly reduced wings acted as braces against the sand. A series of short, rapid jerks ensued, shaking the upper portion of her body violently and causing her abdomen to become completely embedded. This was followed by a rest. The insertion phase lasted from 27 to 73 seconds.

Withdrawal. The abdomen was slowly withdrawn from the sand. This took between 10 and 45 seconds.

Comparative oviposition behaviour

Approach. A direct, short, forwardly-directed walk is probably the most primitive in Therevidae. The forwardly-directed walk of *Thereva*, *Lyneborgia*, and *Pherocera* is replaced by the more advanced backwardly-directed walk in *Phycus*. At the same time, the straight directional walk of *Thereva* and *Lyneborgia* is replaced by the more specialized meandering walk in *Pherocera*. The unmodified walk using all three pairs of legs in *Thereva* and *Phycus* is modified in *Lyneborgia* (hind legs dragged) and *Pherocera* (fore legs used as sensors).

Stance. An upright stance with the abdomen arched so that it enters the substrate, with the hind legs spread outward and slightly hindward in support of the boring abdomen, is probably the most primitive in Therevidae. The arched abdominal position held by *Thereva*, *Phycus*, and *Lyneborgia* is replaced by the more specialized, low profile abdominal position in *Pherocera*. The more primitive hind leg position assumed by *Thereva* (i.e. legs balancing body and thorax, not thrust behind abdomen) is replaced in *Phycus*, *Lyneborgia*, and *Pherocera* by the more specialized hind leg position (i.e. legs placed behind tip of abdomen).

Insertion. A direct insertion of the abdomen into the substrate aided only by abdominal contorting and boring is undoubtedly the most primitive in Therevidae. Primitively, the hind legs are used only to achieve balance, as in *Thereva*. In *Lyneborgia* the hind legs are alternately tensed, and this tensing aids in embedding the abdomen in the substrate. It seems to me that this is specialized with respect to *Thereva*. In *Phycus* and *Pherocera* the hind legs are used for digging a pit or trench, probably the most specialized state of hind-leg activity in the insertion phase. Both *Pherocera* and *Phycus* scoop the substrate towards the body; *Phycus* draws it under the abdomen (more primitive) while *Pherocera* draws it under the thorax (more specialized). Furthermore, *Pherocera* forms a single conical pit while *Phycus* forms a medial conical pit plus sideward and anteriorward trenches from the pit (fig. 36). In the form of pit-making, it is not possible to deduce which is more specialized even though the pit of *Phycus* is more complex. The primitive boring and contorting abdominal insertion motion in *Thevera* is, after various pit-making preliminaries, retained by *Pherocera*. Because of its sharply tapered terminal sclerites (especially t8 and s8) (fig. 20), however, *Pherocera* is able to bury most of its abdomen below the pit-bottom with a minimal amount of abdominal contortion. *Lyneborgia*, by rearing up and vibrating its entire body, inserts the abdomen fully into the substrate. This extreme form of insertion is greatly aided by the enlarged spines on s8. The body-vibrating mechanism is definitely specialized. *Phycus* does not insert its abdomen into the substrate; it merely allows the pit-sides to collapse on the extruded egg. This too, must be considered specialized.

The large spines on t10 (acanthophorites) in *Thereva* must aid considerably in the boring activity. I consider the thickened posterodorsally placed spines (fig. 1, b_1) act more as an anchoring mechanism when tensed, holding the abdomen in the substrate during the contortion motion, in effect embedding the abdomen even further into the substrate. The longer spines (fig. 1, b_2) probably act as opposing anchors. Even though they are thinner, b_2 setae apparently lack the socket mobility of b_1 setae. Upon withdrawal, I would expect the b_1 setae to relax and the abdomen to slide easily out of its inserted position.

Withdrawal. A simple extraction of the abdomen from its fully inserted position is primitive. With the exception of the relaxation of b_1 setae mentioned above, *Thereva* must be considered to possess a primitive withdrawal mechanism. *Lyneborgia* also seems to have a primitive withdrawal. In *Pherocera* this simple withdrawal is coupled with streamline morphology and a complex pit-filling behaviour. *Phycus* does not insert its abdomen, but the continued backwards walk and staccato motion bury the egg and obliterate the pit. This, too, must be considered somewhat specialized.

PHYLOGENETIC ASSESSMENT

It is, of course, inpossible to construct a good phylogeny based solely on oviposition behaviour and morphology of the female terminalia. It is, however, an aid. Most of the current suprageneric taxonomy is based primarily on the morphology of the female and male terminalia. Moreover, the female terminalia and, so it seems, the oviposition behaviour, are very conservative, varying only slightly in related genera. Therefore, it seems plausible that a phylogenetic assessment of the characters discussed under the morphology and oviposition behaviour sections might throw considerable light on the true phylogeny of the Therevidae. It was with this thought in mind that this section was written.

Below are listed various characters along with their plesiomorphic or primitive (○) and apomorphic or specialized (●) states (*see* Hennig 1966). All except the first character are strictly confined to the oviposition behaviour or to the morphology of the female terminalia. The first character refers to an attribute of the pregenital abdominal segments of both sexes of Therevidae and has, to my knowledge, not heretofore been used as a suprageneric character:

1. Pregenital abdominal segments with spiracles
   - ○ in the pleural membrane,
   - ● incorporated in the tergal sclerites.
2. Ratio of medial length to maximum width of tergite 8 is
   - ○ between 0,6 and 0,8,
   - ● less than 0,6 and greater than 0,8.
3. Sternite 8
   - ○ without elongate, strong setae,
   - ● with elongate, strong setae.

4. Posterior portion of sternite 8
   - ○ normal, without hump-like knobs,
   - ● with a single medial or a pair of mediolateral humps.
5. Intersegmental membrane between sternite 8 and the furca
   - ○ unsclerotized and not easily detectible,
   - ● sclerotized, obvious.
6. Tergites nine and ten
   - ○ distinctly separate sclerites,
   - ● fused over part of their common margin.
7. Tergite nine and furca
   - ○ firmly united along posterolateral margins,
   - ● membranously united or not united along posterolateral margins.
8. Furca
   - ○ entirely membranous centrally,
   - ● with a horizontal sclerotized portion medially.
9. Spermathecae
   - ○ heavily sclerotized,
   - ● thinly sclerotized.
10. Tergite ten with setae
    - ○ somewhat specialized,
    - ● lacking or very specialized.
11. Tergite ten
    - ○ longitudinally split into two sclerites or not united with t9,
    - ● a single sclerite united with t9.
12. Subanal plate
    - ○ a single sclerite,
    - ● longitudinally split into two distinct sclerites.
13. Cerci
    - ○ separate and distinct sclerites,
    - ● united into a single common sclerite.
14. The walk of the approach phase in oviposition directed
    - ○ forward,
    - ● backward.
15. The walk of the approach phase of the oviposition sequence completed
    - ○ on all three pairs of legs,
    - ● on only two pairs of legs.

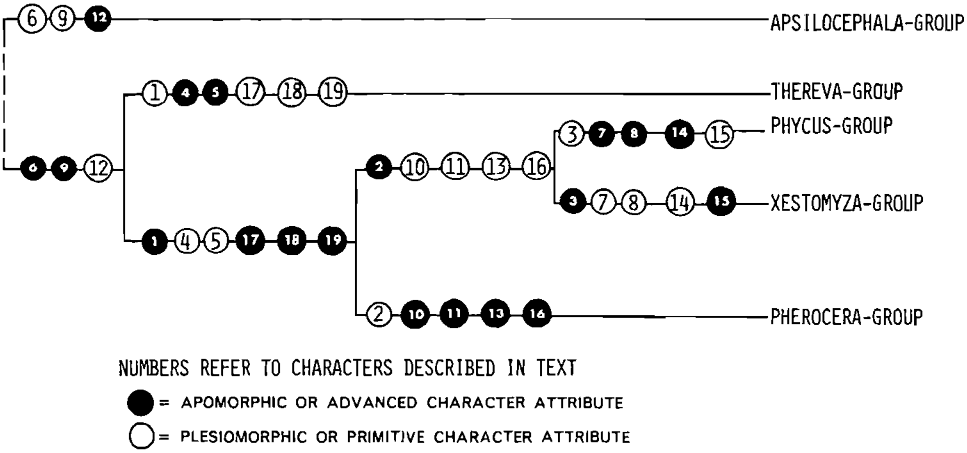
16. In the stance phase of one oviposition sequence, the abdomen
    ○ arches strongly downward at its tip, the apex contacting the substrate,
    ● maintains a low profile position, most of its length contacting the substrate.

17. In the stance phase of the oviposition sequence, the hind legs are
    ○ not extended behind the tip of the abdomen,
    ● extended behind the tip of the abdomen.

18. Insertion of abdomen into substrate is
    ○ aided only by abdominal contorting and boring,
    ● aided by hind legs (pulling or digging).

19. Withdrawal of the abdomen is accompanied by
    ○ no leg or body action to cover eggs,
    ● leg and/or body action to cover eggs and pit.

The following diagram represents my current ideas about the phylogenetic relationships of the genus-groups herein discussed. This diagram is constructed with both morphological and ethological information, but is virtually confined to attributes of the female terminalia and the oviposition sequence.



DISCUSSION

It has been noted that within the Asiloidea, oviposition substrate and behaviour could be deduced from a study of the structural modifications of the female terminalia, and vice versa (i.a. Melin 1923; Hesse 1969; Wilcox & Papavero 1971; Irwin 1973). The correlation between oviposition in loose soil or sand and the circlet of strong spines (setae) at the apex of the abdomen (t10) has often been presented as evidence in support of the above supposition. Although members of the *Thereva*-group with well-developed b_1 and b_2 setae on t10 (figs 1, 14, 33) oviposit in loose soil and sand, my studies do not entirely support the correlation. A considerable number of therevids which either lack setae or possess only weak setae on t10 also oviposit in loose soil or sand. In fact, as far as is now known, all therevids lay eggs one at a time and oviposit in soil or sand; and upon completion of the oviposition sequence, the eggs are thinly covered by the substrate.

The major methods of ovipositing in loose soil or sand have been discussed under 'comparative oviposition behaviour—insertion and withdrawal'. The strong b_1 and weaker b_2 setae of t10 in the *Thereva*-group undoubtedly aid in embedding the abdomen in the substrate. How this is accomplished can, as of now, only be deduced. It seems probable that the setae serve more as anchoring devices than as digging apparatus. Successive waves of abdominal contortions effectively embed the abdomen, but unless there was an anchoring mechanism, the abdomen would become dislodged while retracting in preparation for each successive contortional wave. The often flattened b_1 setae almost certainly aid in anchoring the abdomen in the substrate between contortional waves.

The strong setae of t10 found in the *Thereva*-group are not evident in the *Xestomyza*-group. Instead, there is a set of strong, recurved spines on s8 (figs 6, 12) which probably act as both a digging apparatus and as an anchoring device during oviposition. During the insertion phase of oviposition, the female rears up and begins to vigorously jerk her entire body. Each forward thrust of her body forces her terminalia, including the spines on s8, backwards slightly. On each successive backward jerk, the terminalia move forward, and, because of their curvature, the spines bite slightly deeper into the substrate. The spines secure the position of the abdomen on each successive jerk, and, at the same time, provide the bite for deeper penetration.

Neither the strong setae on t10 found in the *Thereva*-group nor the strong spines on s8 found in the *Xestomyza*-group are evident in the *Phycus*-group or the *Pherocera*-group. Upon morphological evidence alone, it would be difficult to speculate on the mode of oviposition into a soil or sand substrate. Both groups, in fact, dig pits with their hind legs. In the *Phycus*-group an egg is laid in the bottom of the exposed pit; abdominal movements bury it. No anchoring device is needed. In the *Pherocera*-group the abdomen is thrust into the bottom of the pit. Since segment 8 is greatly streamlined (figs 9, 10), a single thrust is sufficient to embed the abdomen completely. Again, an anchoring device is not needed. The female in the *Pherocera*-group fills in the pit with her hind legs once her abdomen is withdrawn. Neither the *Pherocera*-group nor the *Phycus*-group possess any obvious morphological modifications towards more efficient digging on the hind legs.

Detailed observations on the oviposition of the Vermileoninae (Tabanoidea: Rhagionidae) (Hemmingsen & Nielsen 1971) have shown that pit forming is not unique to any single group. That the Vermileoninae and the *Pherocera*-group plus *Phycus*-group of the Therevidae possess convergent behaviour patterns with respect to certain aspects of pit digging becomes apparent when the gross patterns are compared. To my knowledge the pit-forming therevids always dig by moving their hind legs and deposit a single egg either in contact with or thrust into the pit bottom. The Vermileoninae, on the other hand, dig a pit by moving their middle legs and eject one or more eggs simultaneously in mid-air which land within the pit. That pit-digging in these two instances is analogous, is certain.

CONCLUSIONS

Ovipositional behaviour seems relatively consistent within any given genus-group, but varies considerably between genus-groups of Therevidae; likewise, certain morphological features of the female terminalia appear to be relatively unchanged within any given genus-group, but vary between genus-groups. Seemingly, a strong correlation exists between certain behavioural adaptations and morphological attributes. This in turn suggests a plausible predictive model relating form and function in the Therevidae. The correlative forms and functions of four different genus-groups have, in effect, been discussed in the text, and they form the basis of the predictive model.

The *Apsilocephala*-group, from the morphological evidence already presented, does not easily fit within the current concepts of the Therevidae, and, in fact, its positive placement within the Asiloidea has been questioned.

Using the predictive model described above, what, if anything, can be said about the oviposition behaviour of the *Apsilocephala*-group? Firstly, the female of the *Apsilocephala*-group lacks strong b_1 setae. She also lacks strong, curved setae on s8. Secondly, there are no apparent morphological adaptations for anchoring the terminalia in the substrate. The entire abdomen appears extremely fragile and weak, and the terminalia are not strongly tapered. Therefore, it seems probable that abdominal contortions do not drive the terminalia into the substrate; furthermore, the abdomen is probably not inserted into the substrate in a single thrust. What remains? From the limited input into the model there are two alternatives. Either the female oviposits by digging a hole with one or more sets of legs or the female does not oviposit into the substrate. If the former is correct, then the digging behaviour may be equivalent to that of the *Phycus*-group or *Pherocera*-group or, like that of the Vermileoninae, may have been acquired independently. If the latter proves correct, then, with respect to their oviposition behaviour as well as terminalia features, the *Apsilocephala*-group would fall outside the boundaries of the predictive model input. Therefore, either of the two alternatives could lead to a similar conclusion: the *Apsilocephala*-group is not closely related to any other genus-group in the Therevidae; that the sister-group of the *Apsilocephala*-group is possibly the rest of the Therevidae, or possibly some group outside the family Therevidae. (If the female digs a pit, it could fit into the phylogenetic scheme of the Therevidae, but the morphology of the female terminalia makes this unlikely.) The phylogenetic chart (page 932) illustrates by a dotted line the uncertain connection between the *Apsilocephala*-group and the rest of the genus-groups of Therevidae herein examined.

ACKNOWLEDGEMENTS

The following persons and institutions are gratefully acknowledged for their generous assistance in the preparation of this manuscript: Dr B. R. Stuckenberg, Director, Natal Museum, Pietermaritzburg, and Dr A. M. Hemmingsen, University Zoological Museum, Copenhagen, for critical comments and invaluable suggestions; Dr Leif Lyneborg, University Zoological Museum, Copenhagen, for companionship in the field and helpful morphological suggestions; Dr M. K. Seely, Director of Research, Namib Desert Research Station, for assistance in the field; Dr E. I. Schlinger, Professor of Entomology, University of California, Berkeley, for invaluable suggestions during the study of *Pherocera* and related Therevidae; Dr Marcos Kogan, Associate Entomologist, Illinois Natural History Survey, Urbana, for critical reading of the manuscript; and my wife Bonnie Jean, for valuable help, constant companionship, and needed encouragement.

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Date received: 29 April 1975